

PALAEOECOLOGICAL ANALYSIS OF AMMONOID ASSEMBLAGES IN THE TURONIAN *SCAPHITES* FACIES OF HOKKAIDO, JAPAN

by KAZUSHIGE TANABE

ABSTRACT. Palaeoecological analysis of ammonoid assemblages in the Turonian (Cretaceous) *Scaphites* facies of Hokkaido has yielded quantitative data on distribution, mode of occurrence, and preservation of many species. The results show that most collignoniceratids, acanthoceratids, and heteromorphs in the region are autochthonous in a broad sense; the litho- and biofacies in which these groups occur suggest that the first two lived in inshore to near-shore shallow waters, and the latter in nearshore to offshore more or less deep waters. Post-mortem transportation or drift might be important as a factor in distribution of thanatocoenoses of the phylloceratids, tetragonitids, and desmoceratids; therefore their habitats could not be determined from the analysis of assemblages. Examination of relative siphuncular strength in many well-preserved specimens of twelve species suggests that the depth limits of the tetragonitids, phylloceratids, and desmoceratids may have been much greater than those of other groups.

RECONSTRUCTION of habitats is one of the most interesting subjects in ammonoid palaeobiology. Recent work on ammonoid palaeoecology has been carried out both from the viewpoint of functional morphology, relying on hydrodynamic experiments (Chamberlain 1971, 1976; Chamberlain and Westermann 1976) and hydrostatic examination (Reyment 1958, 1973; Heptonstall 1970; Westermann 1971, 1972, 1973, 1975a, b; Tanabe 1977a), and from comparative morphology and anatomy (Mutvei 1964, 1967, 1975; Jordan 1968; Stürmer 1970; Lehmann 1970, 1971, 1972, 1975, 1976; Kaiser and Lehmann 1971; Lehmann and Weitschat 1973; Mutvei and Reyment 1973).

From these studies various aspects of ammonoid palaeoecology have been clarified, but opinions remain divided on the habitat and bathymetric distribution as well as the mode of life of the group. The main reason for this is probably related to limitations in methodology, since analogies with the ecology of living relatives present various restrictions in reconstructing the palaeoecology of extinct animals. For this reason, both functional morphological and assemblage palaeoecological approaches are needed. Most previous studies on functional morphology have been based on small collections or idealized models, and little attention has been paid to actual ammonoid assemblages.

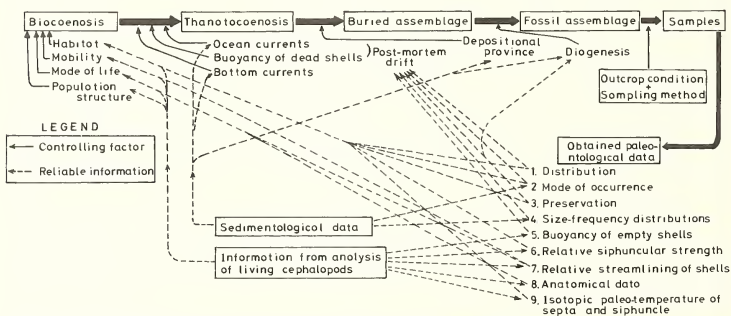
Although the geographical change in faunal composition of ammonoid assemblages in relation to litho- and biofacies has been examined by such palaeontologists as Scott (1940), Westermann (1954), Fischer (1967), Ziegler (1967), Torrens (1967), Hallam (1969, 1971), Wendt (1971), Kennedy and Cobban (1976), Obata and Futakami (1977), and Matsumoto (1977b), palaeoecological analysis of such assemblages has not yet been satisfactorily attempted, apart from the excellent work by Kauffman (1967) in the Western Interior of the U.S.A. This paper presents the results of analysis

of geographical distribution and mode of occurrence of ammonoids in the Turonian of Hokkaido, together with quantitative data from assemblage analysis in the Middle Turonian *Scaphites* facies in selected areas. Relative siphuncular strength is also examined in many well-preserved specimens of some Turonian species from the region to determine the relative inhabitable depth limits of ammonites. The presumed habitats and problem of post-mortem drift and transportation of ammonoid shells are discussed in the light of these analyses.

PALAEOECOLOGICAL SIGNIFICANCE OF AMMONOID ASSEMBLAGE ANALYSIS

It is evident that the ultimate objective of assemblage analysis for planktonic or nektonic animals differs from that for benthonic ones. Most previous palaeoecological work on marine benthonic fossils has had as its aim the recognition of communities. In contrast, it is difficult to reconstruct the biocoenosis of planktonic or nektonic fossils, reflecting the original community, because of their mobility in life and the effects of post-mortem transportation. It has long been accepted that most ammonoids were probably planktonic or nekto planktonic, because of their fundamental similarity to living *Nautilus*. This implies that the life habitat was more widespread than that of benthonic animals. Moreover, the effect of post-mortem drift should be taken into consideration for the reconstruction of ammonoid habitats and the determination of biogeographical distribution patterns.

The transition from biocoenosis to fossil assemblage, and the various factors involved in this process, are illustrated in text-fig. 1. The distribution pattern of living ammonites was probably controlled by such biological factors as habitat, mode of life, mobility, and population structure. The post-mortem transportation of ammonoid shells, especially necroplanktonic drift, may have had an important role in the formation of death assemblages (Reyment 1958; Kennedy and Cobban 1976).



TEXT-FIG. 1. Simplified diagram showing the transition from ammonoid biocoenosis to fossil ammonoid assemblage, with the various factors involved.

It is well known that most dead shells of *Nautilus pompilius* Linné are concentrated close to their original habitat belts around the earth's circumference, and that occasionally some of them drift for a long distance on ocean currents (Hamada 1964; Teichert 1970). More than forty examples of *N. pompilius* carried by drift have been reported from the Japanese Islands since 1843 (Hamada 1965). However, this number is small when compared with the abundant occurrence of dead shells in the south-west Pacific and Indian Oceans where living *N. pompilius* occur.

The extent of post-mortem drift in ammonoids was probably influenced by their shell buoyancy, the mechanical strength of the septa, and the siphuncle. Palaeontological data which can be obtained from a fossil sample are summarized as points 1 to 9 in text-fig. 1. Of these the data on mode of occurrence, distribution, and preservation of a species, and relationships with lithofacies, are the most useful factors to use as a reliable basis to infer ammonoid habitat and the extent of post-mortem transportation. Functional morphological and comparative anatomical approaches are similarly useful to determine the mode of life, feeding habits, and life attitude of ammonoids.

The following conditions are necessary in order to make reliable palaeoecological analyses of ammonoid assemblages.

1. Extensive outcrops of ammonoid beds must be available in a given depositional province.
2. Well-preserved specimens are required from various localities of the same age.
3. Precise age determination and inter-regional correlation of the ammonoid-bearing beds must be made.

The Upper Cretaceous ammonoid assemblages in the meridional zone of Hokkaido come close to satisfying these conditions; i.e. specimens are fairly common throughout the sequences in various areas, and most occur in calcareous marly or sandy concretions and are well preserved. Moreover, as a result of studies of sedimentary facies (Tanaka 1963, 1970; Matsumoto and Okada 1973), palaeocurrent directions (Tanaka 1970), and petrography of the clastic rocks (Matsumoto and Okada 1971), it has become clear that the lateral change from inshore 'shelf' facies to offshore flysch can be recognized from west to east in the Upper Cretaceous marine basin of central Hokkaido. It is possible, therefore, to examine the lateral change in ammonoid assemblages with sedimentary facies.

Precise intra-regional lithostratigraphical correlation of the ammonoid-bearing beds is difficult because of the complicated geological structure, lack of key marker beds, and the remarkable lateral change in lithofacies. At present, short-ranged and widely distributed zonal indices such as inoceramid species are most useful for the dating and correlation of the ammonoid-bearing beds.

The lateral changes in sedimentary facies are particularly conspicuous in the Turonian, where various kinds of ammonoids occur abundantly, and thus these assemblages of Hokkaido are the basis of the present study.

DISTRIBUTION OF AMMONOID SPECIES

Note on the Turonian Scaphites facies. Tanaka (1963), Matsumoto and Okada (1973), and Obata and Futakami (1977) have made preliminary observations on the lateral changes in ammonoid assemblages associated with sedimentary facies in the Upper Cretaceous of Hokkaido. The assemblages, characterized by the abundance of

scaphitids, are recognized occasionally in the silty to fine sandy facies of the Cenomanian to Coniacian, and the whole litho- and biofacies have been termed the *Yezoites* (= *Scaphites*) beds (Yabe 1927; in the strict sense Yabe proposed the *Yezoites* beds as the local biostratigraphical unit) and the *Scaphites* facies (Matsumoto and Okada 1973) respectively. According to Matsumoto and Okada the *Scaphites* facies represents a biofacies intermediate to the nearshore shelf facies and offshore flysch. This seems to correspond roughly with the *Baculites* facies of Matsumoto and Obata (1962).

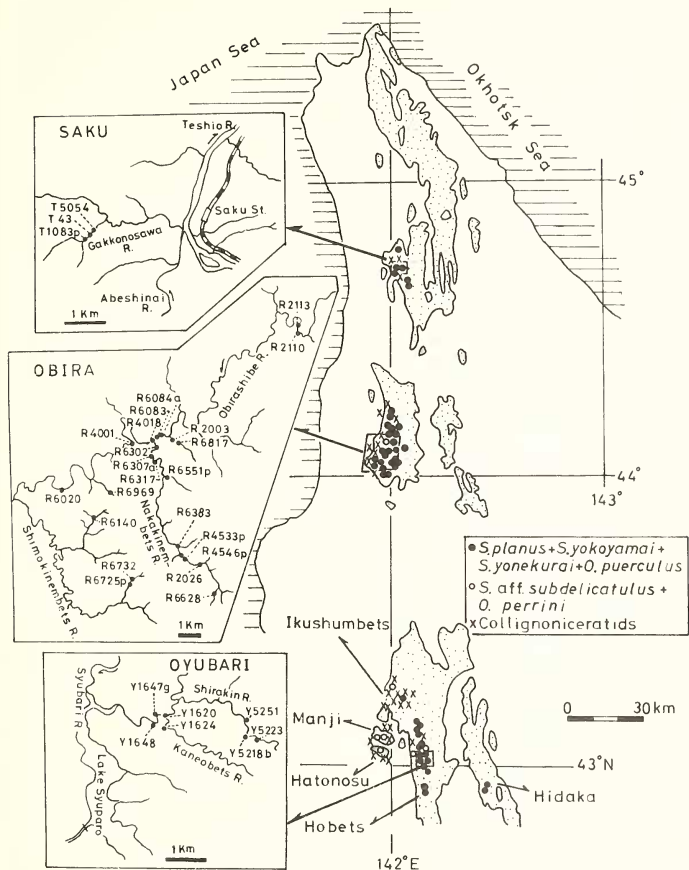
I have previously discussed the classification and geographical and stratigraphical distributions of the Middle Cretaceous Scaphitidae in the North Pacific region (Tanabe 1977b), summarizing the frequency of occurrence of described species in selected areas of Hokkaido and south Sakhalien. Text-fig. 2 shows geographical distribution of scaphitids and collignoniceratids as plotted for the present assemblage analysis. The scaphitids occur abundantly in the western belt of the meridional Cretaceous zone of Hokkaido, especially in the Saku, Obira, and Oyubari areas. The Middle to Upper Turonian in these areas is characterized by silty mudstone, sandy siltstone, and intercalated sandstone and conglomerate lithologies, and has been defined by Matsumoto (1942) and Matsumoto and Okada (1973) as a local litho-stratigraphical unit termed the Saku Formation. Numerous ammonoids including the scaphitids, and inocerami and other molluscs, together with drifted plant fragments occur in calcareous concretions in this formation. In general, fossiliferous calcareous concretions are found more abundantly in fine-grained rather than coarse-grained sediments; however, they are distributed randomly or in layers throughout the Turonian sequences in the areas studied. The scaphitids in the formation are represented by *Scaphites planus* (Yabe), *S. yokoyamai* Jimbo, *S. aff. subdelicatus* Cobban and Gryc, *S. yonekurai* Yabe, *Otoscapites puerculus* (Jimbo), and *O. perrini* (Anderson).

The ammonoid assemblages associated with the scaphitids are also recognized in the fine-grained sandstone or silty sandstone lithologies of the Middle to Upper Turonian of the Manji, Pombets, and Hatonosu (= Yubari) areas of central Hokkaido (see text-fig. 2). The scaphitids in these areas are only *S. aff. subdelicatus* and *O. perrini*.

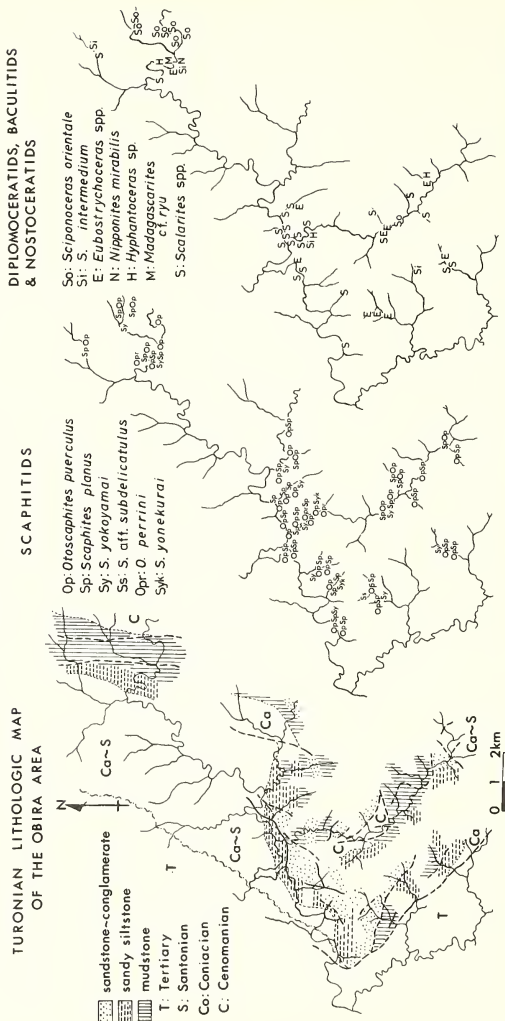
Distribution of ammonoid species in the Turonian of Hokkaido. Taking the Obira area of north-western Hokkaido and the Manji-Ikushumbets-Oyubari-Hobets areas as examples, the distribution pattern and the mode of occurrence of ammonoids in the Turonian are described here.

Tanabe *et al.* (1977) collected more than 5000 ammonoid individuals belonging to fifty-seven species of thirty-seven genera from 177 Turonian localities in the Obira area. On the basis of this work, a Turonian lithological map and the occurrences of twenty-nine selected species are shown in text-figs. 3 and 4.

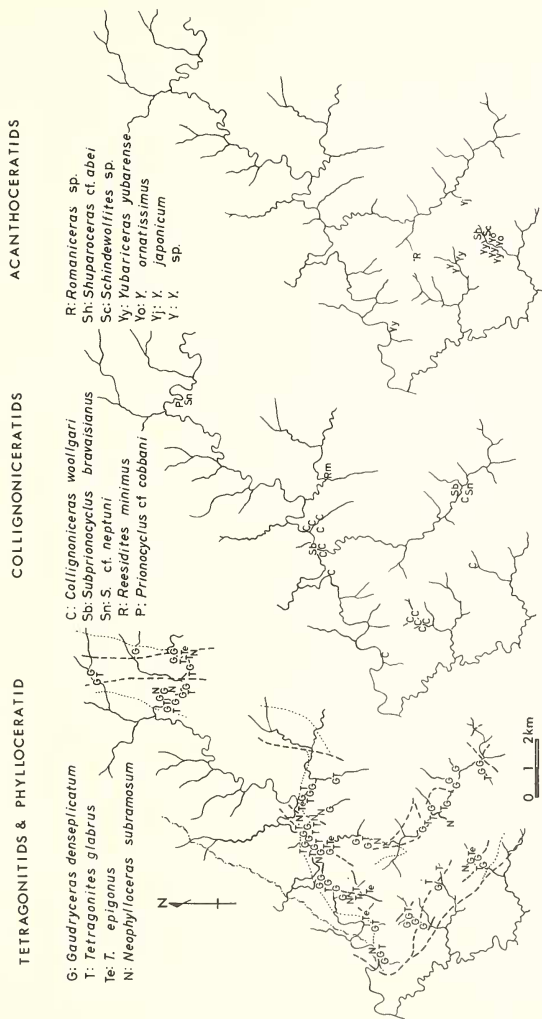
According to Tanaka (1963) and Tanabe *et al.* (1977), the Turonian in this area has a maximum thickness of about 1200 m consisting of mudstone, sandy siltstone, tuffite, and intercalated sandstone and conglomerate. There is a considerable lateral change of lithofacies in the Middle to Upper Turonian, and the sediments tend to be coarser and thinner moving from north-east to south-west.



TEXT-FIG. 2. Map of central Hokkaido showing outcrops of post-Albian marine Cretaceous deposits (dotted), geographical distribution of Turonian scaphitids and collignoniceratids, and locations of ammonoid samples studied.

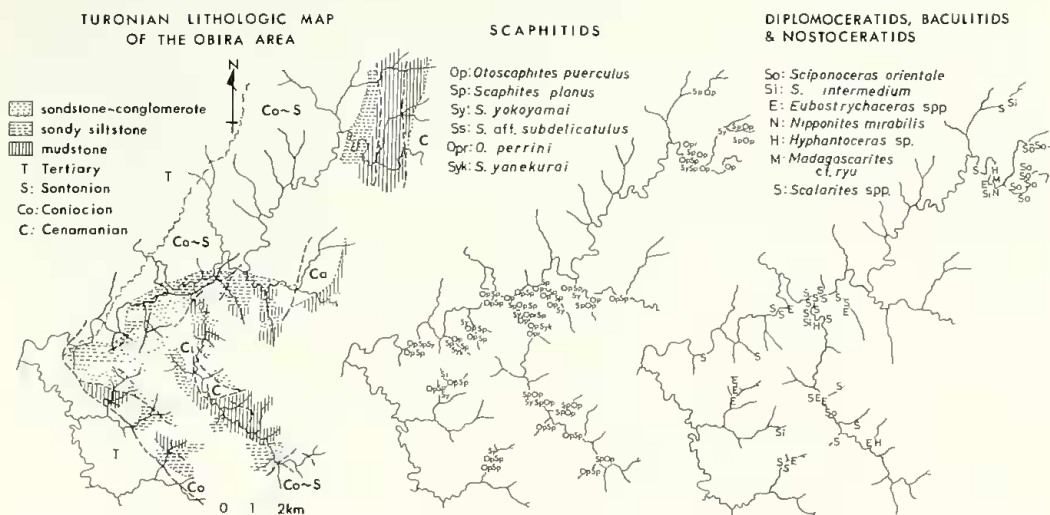


TEXT-FIG. 3. Distribution pattern of heteromorph ammonites in relation to lithofacies in the Turonian of the Obira area, north-western Hokkaido.

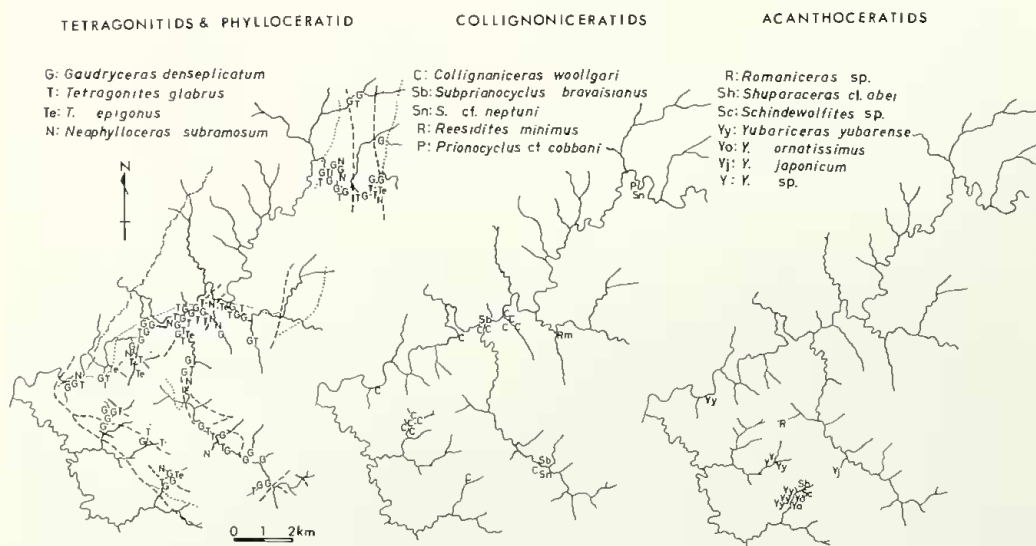


TEXT-FIG. 4. Distribution pattern of the tetragonitids, desmoceratids, phylloceratid, collignoniceratids, and acanthoceratids in relation to lithofacies in the Turonian of the Obira area. See text-fig. 3 for lithological map.





TEXT-FIG. 3. Distribution pattern of heteromorph ammonites in relation to lithofacies in the Turonian of the Obira area, north-western Hokkaido.



TEXT-FIG. 4. Distribution pattern of the tetragonitids, desmoceratids, phylloceratid, collignoniceratids, and acanthoceratids in relation to lithofacies in the Turonian of the Obira area. See text-fig. 3 for lithological map.

Species of Tetragonitidae [*Tetragonites glabrus* (Jimbo), *T. epigonus* (Kossmat) and *Gaudryceras denseplicatum* (Jimbo)] and Phylloceratidae [*Neophylloceras subramosum* Spath] show a widespread and random distribution pattern regardless of sedimentary facies. The frequency of occurrence at each locality is generally low.

The scaphitids are one of the most important ammonoid groups in the Turonian. They are distributed throughout the Obira area, but occurrence is restricted to silty mudstone to sandy siltstone lithofacies. Other heteromorph ammonites also occur abundantly in the silty facies with the scaphitids. *Sciponoceras orientale* Matsumoto and Obata is found in the claystone of the Lower Turonian in the north-eastern area.

In contrast, the distribution pattern of the collignoniceratids and acanthoceratids is quite different from those of other ammonoids. Both groups are common in the fine-grained sandstone and sandy siltstone lithologies in the south-western area, but are rare in the north-east. *Collignoniceras woollgari* (Mantell) and *Subprionocyclus bravaisianus* d'Orbigny occur abundantly at several localities, but not together.

The above-mentioned general characteristics in distribution and mode of occurrence of ammonoids in the Obira area are also recognized in the Upper Turonian of the Manji-Ikushumbets-Oyubari-Hobets areas. Text-fig. 5 shows the geographical variation of faunal composition at family or subfamily level in the selected nine regional ammonoid sample groups. According to Matsumoto (1942, 1965), and Obata and Futakami (1977), the sediments of the Upper Turonian in these areas tend to become coarser and thinner from east to west. The assemblages in the western region are characterized by the dominant occurrence of the collignoniceratids, whereas the heteromorphic ammonites, tetragonitids, phylloceratids, and desmoceratids predominate in the east.

ANALYSIS OF AMMONOID ASSEMBLAGES

For this study thirty-two ammonoid samples comprising 1794 individuals of twenty-three species from the middle to upper part of the Middle Turonian *Inoceramus hobetsensis* Zone of the Saku, Obira, and Oyubari areas have been examined quantitatively. The locations of samples examined are shown in text-fig. 2. Each sample was collected from a single calcareous concretion, and is represented by more than ten individuals. The species composition and frequency of occurrence are summarized in Table 1.

Comparison of species composition between a sample pair. Firstly, the similarity of species composition between sample pairs was investigated using Kimoto's (1967) similarity index for the twenty samples of more than thirty individuals.

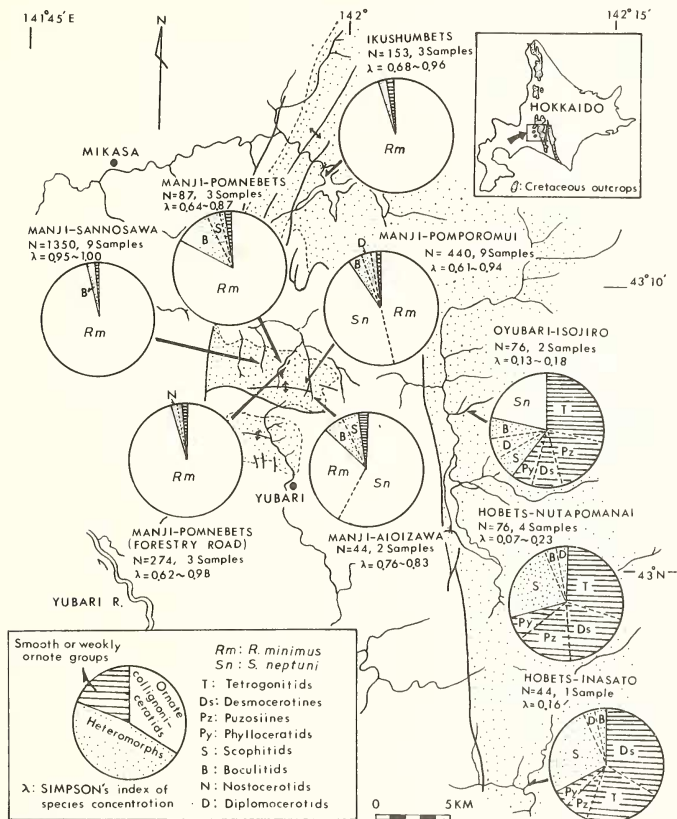
According to Kimoto, the similarity index (C_{π}) is given by the following formula.

$$C_{\pi} = \frac{2 \sum_{i=1}^s n_{1i} n_{2i}}{\left(\sum_{i=1}^s \frac{n_{1i}^2}{N_1} + \sum_{i=1}^s \frac{n_{2i}^2}{N_2} \right) N_1 N_2}$$

where N_1 and N_2 are the total numbers of individuals in two samples, n_1 and n_2 are numbers of individuals of i -number species in two samples, and s is the total number

of species constituting two samples. C ranges from 0 to 1, and if two samples are identical in respect of species composition ($N_1 = N_2$ and $n_1 = n_2$), C_π is equal to 1.

The results of this analysis are summarized in Table 2. Strong similarity is observed in each pair among the samples, except for R2003, R6628, and R4001. More than 70% and 30% of the total combinations give a C_π value of over 0.7 and 0.9



TEXT-FIG. 5. Geographical variation of faunal composition at family or subfamily level, and Simpson's (1949) index of concentration (λ) in the nine selected regional ammonoid sample groups from the Upper Turonian of central Hokkaido.

TABLE 1. Species composition and Simpson's (1949) index of concentration in the thirty-two ammonoid samples from the Middle Turonian *Scaphites* facies of the Saku, Obira, and Oyubari areas, Hokkaido.

Area	Saku										Obira										Oyubari										Total no. of specimens	
Locality (=sample number)	T1083p	T 43	T 5054	R 2110	R 6732	R 2003	R 4533p-1	R 4078p	R 2113	R 6628	R 4001	R 4546p	R 2026	R 6302	R 6377	R 6084p	R 6307b	R 6020	R 6969	R 6083	R 6383	R 6817	R 6725p	Y1648	Y1670	Y1624	Y1625	Y1626b	Y16223	Y1647g		
Species																																
<i>Otoscaphtes puerulus</i> (Jimbo)	34	41	14	209	89	24	31	11	19	18	4	8	11	19	17	4	9	10	12	5	3	1	25	10	12	22	22	9	1	1	700	
<i>Scaphites planus</i> (Yabe)	45	15	10	156	110	14	39	18	16	18	3	3	11	16	13	12	3	8	10	5	5	3	30	30	9	16	9	3	1	1	623	
<i>Damesites ainuanus</i> Matsumoto				16	3	12	10	1	3	6	21	14	2	2	4	3	1	1	2	2	2	1	2	4	4	1	1	1	1	1	104	
<i>Scaphites</i> sp.				1	5	8	5	4	2	1	1	3	4	2	1	1	1	1	1	1	1	1	2	1	4	3	3	3	5	1	63	
<i>Neophylloceras subramosum</i> Spath	9	1	1	6	3	3	3	3	5	2	2	2	1	1	1	1	1	1	1	1	1	1	2	3	3	1	1	1	1	1	46	
<i>Tetragonites glabrus</i> (Jimbo)					1	2		8	6	1	1	3	1	2	1	1	1	1	1	1	1	1	6	2	3	1	1	1	1	1	42	
<i>Subprionocyclus bravaianus</i> D'Orbigny					2	3	39																								38	
<i>Gaudryceras densapicatum</i> (Jimbo)								6	1	1	3	2	2			1	1	1	1	1	1	2	1	3	3	4					34	
<i>Scaphites yokoyamai</i> Jimbo	1			3	9	1	2	6							7																23	
<i>Eubastrioceras</i> sp.				4									3	1	1	3										4	5					22
<i>Mesapuzosia</i> sp.	5	1						4																							5	
<i>Mesapuzosia pacifica</i> Matsumoto					1	1																										2
<i>Yubariceras yubarense</i> Mat. Saito & Fukada																																7
<i>Collignoniceras woolgari</i> (Mantell)																																6
<i>Scaphites yonekurai</i> Yabe	1			2											3																	3
<i>Otoscaphtes perrini</i> (Anderson)																																1
<i>Tetragonites epigenus</i> (Kossmat)																																1
<i>Anagaudryceras limatum</i> (Yabe)																																4
<i>Madagascanites cf. ryu</i> Mat. & Muramata																																3
<i>Mesapuzosia yubarensis</i> (Jimbo)																																4
<i>Hyphantoceras</i> sp.					3																											3
<i>Sciponoceras intermedium</i> Mat. & Obata																																1
<i>Phyllophyceras ezoense</i> Yokoyama																																1
Number of specimens at each locality	95	62	26	409	227	93	90	61	51	47	37	36	36	36	35	31	29	24	23	18	16	14	12	10	10	78	52	45	43	19	18	1794
Simpson's (1949) index of concentration	36	49	42	41	39	26	31	15	25	31	34	21	22	46	22	43	10	27	44	17	38	23	20	11	22	25	37	14	39	37	18	

respectively. This evidence suggests that most of the ammonoid assemblages in the Middle Turonian *Scaphites* facies of the Saku, Obira, and Oyubari areas are closely similar in species composition.

Frequency of occurrence of each species in selected samples. To analyse the relative density ratios among the species constituting the assemblages, 95% confidence limits of population occurrence of each species have been examined in seven samples (T43, T1083p, R2110, R6732, R4533p-1, R2113, and Y1648) with similar species compositions; the results are shown in text-fig. 6. Both *Scaphites planus* and *Otoscaphtes puerulus* have a frequency of more than 20% (lower limit) in every sample, and are regarded as the characteristic species in each sample.

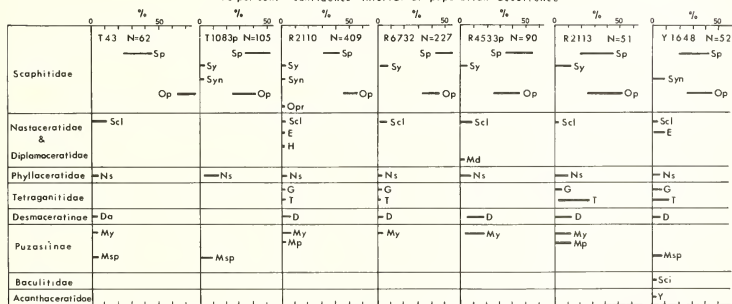
By comparison with these two species, the frequency of other species is generally low, though *Tetragonites glabrus*, *Neophylloceras subramosum*, and *Damesites ainuanus* Matsumoto also reach the upper limit of confidence of more than 10% in certain samples. As seen in Table 1, the frequency of occurrence of *O. puerulus* and *S. planus* is not so high in samples R2003, R6628, and R4001.

Species diversity. Frequency of occurrence of each species in a sample gives a measure of species diversity in an assemblage. Simpson's (1949) index of concentration is one of the most effective methods of expressing this species diversity. It ranges from 0 to 1, and if the diversity of a sample becomes smaller in accordance with an increase of proportion of number of specimens of a predominant species to total sample size, it gradually increases and approaches 1 (see Kimoto 1976, Table 2-1). The results of this method as applied to the samples examined are shown at the bottom of Table 1. Every sample has an index of concentration of less than 0.5; hence the species diversity in the ammonoid assemblages of the Middle Turonian *Scaphites*

TABLE 2. Kimoto's (1967) similarity index for species composition between a pair of samples among the selected twenty ammonoid samples of more than thirty individuals.

[illegible]

95 per-cent confidence interval of population occurrence



Sp: <i>Scaphites planus</i>	Opr: <i>Otocaphites perrini</i>	Ma: <i>Madagascarcites</i> cf. <i>Ryu</i>	D: <i>Damites ainanus</i>	Sc: <i>Sciponoceras intermedium</i>
Sy: <i>Scaphites yokoyamai</i>	Sc: <i>Scalarites</i> sp.	No: <i>Neophylloceras subramosum</i>	My: <i>Meopuzosia yubarenis</i>	Mo: <i>Meopuzosia pacifica</i>
Syn: <i>Scaphites yokuraku</i>	E: <i>Eubastriochoceras</i> sp.	G: <i>Gadryoceras densilocat</i>		Y: <i>Yubariceras yubarense</i>
Opr: <i>Otocaphites puerulus</i>	H: <i>Hyphantoceras</i> sp.	T: <i>Tetragonites glabrus</i>	Meop: <i>Meopuzosia</i> sp.	

TEXT-FIG. 6. 95% confidence interval of population occurrence of species in the seven selected ammonoid samples from the Middle Turonian of the Saku, Obira, and Oyubari areas. N = sample size.

facies in the Saku, Obira, and Oyubari areas can be regarded as relatively high. In contrast, the Upper Turonian ammonoid assemblages in the Manji and Ikushumbets areas of central Hokkaido, which are characterized by the abundant occurrence of collignoniceratids, have a very low species diversity (text-fig. 5).

Interspecific overlap among samples. Various methods have been proposed to classify animal communities on the basis of similarity in species composition. Among these, the index for degree of interspecific overlap is superior to the common species method (e.g. Jaccard's and Simpson's coefficient) for the comparison of two geographically contiguous communities, because it takes into account both number of species and number of individuals. Even if objective fossil assemblages are allochthonous, as are most ammonoid assemblages, characteristics of species composition of each assemblage can be recognized, allowing comparison of the pattern of interspecific overlap among species with the aid of this method when many samples are obtained from various localities at a definite horizon.

Morishita's (1959) index for degree of interspecific overlap is little influenced by sample size. Using this method, the interspecific overlap among the twenty-two species in the samples was examined, and the results are summarized in Table 3. The twenty-two species, all of which are represented by more than three individuals, may be divided into the following three groups by the similarity in pattern of overlap with other species.

GROUP A: phylloceratid, tetragonitids, desmoceratines, and puzosiines (*Neophylloceras subramosum*, *Tetragonites glabrus*, *T. epigonus*, *Gaudryceras denseplicatum*, *Anagaudryceras limatum* (Yabe), *Damesites ainuanus*, *Mesopuzosia pacifica* Matsumoto, and *Mesopuzosia* sp.). Every species is a smooth or weakly ornate morphotype.

GROUP B: heteromorph ammonites belonging to the Scaphitidae, Baculitidae, Nostoceratidae, and Diplomoceratidae (*Scaphites planus*, *S. yokoyamai*, *S. yonekurai*, *Otoscapites puerculus*, *O. perrini*, *Sciponoceras intermedium* Matsumoto and Obata, *Eubostriyoceras* sp., *Hyphantoceras* sp., *Madagascarites* cf. *ryu* Matsumoto and Muramoto, and *Scalarites* sp.).

GROUP C: collignoniceratids and acanthoceratid (*Collignoniceras woollgari*, *Subprionocyclus bravaisianus*, and *Yubariceras yubarensis* Matsumoto, Saito and Fukada). Every species has a strongly ornate shell morphology. The first- and last-named species occur in the lower to middle part of the Middle Turonian of the Obira area, while the middle one is restricted to the upper part.

Species belonging to Group A are characterized by a high degree of co-occurrence with other species within the group at various localities. *Mesopuzosia yubarensis* (Jimbo) has a higher value of Morishita's index more comparable with heteromorph ammonites than with the species belonging to Group A, and it was thus excluded from this group.

Species in Group B similarly show a high degree of overlap with other species of the same group and also with those of Group A. It is worthy of notice that the degree of overlap is particularly great between any two of *N. subramosum*, *G. denseplicatum*, *T. glabrus*, *Scaphites planus*, *O. puerculus*, and *Scalarites* sp.

Group B may be subdivided into the combination of *Scaphites planus*, *S. yokoyamai*, *S. yonekurai*, *O. puerculus*, *Eubostriyoceras* sp., *Hyphantoceras* sp. and *Scalarites* sp., and that of *O. perrini*, *Madagascarites* cf. *ryu*, and *Sciponoceras intermedium*. The latter subgroup has a lower value of Morishita's index with other species than the former.

TABLE 3. Morishita's (1959) index for degree of interspecific overlap in occurrence among the twenty-two species constituting the thirty-two ammonoid samples studied. C_g at the bottom of this table gives the value of Morishita's index.

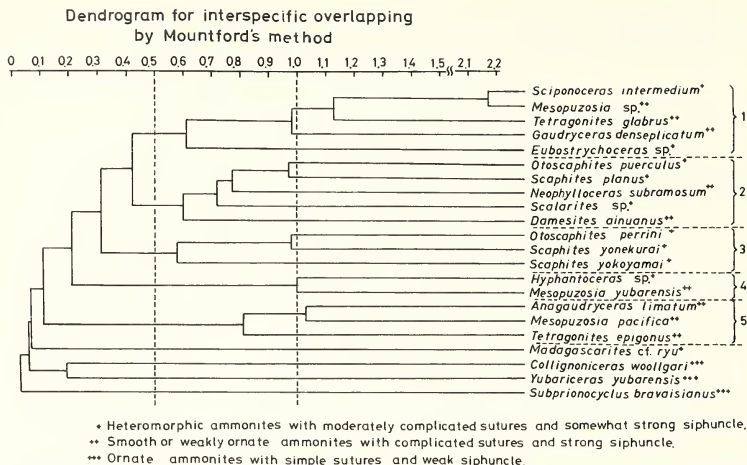
Morishita's index for degree of overlap

	Heteromorphic ammonites										Smooth or weakly ornate ammonites										Strongly ornate ammonites	
	Op	Sp	Syk	Syn	E	Scl	H	Opr	Md	Scl	Ns	Gd	Tg	Te	Al	Da	Msp	Mp	My	Sb	Cw	Yy
<i>O. puerulus</i> (Op)		●	●	●	●	●	●	●	x	x	●	●	x	x	x	●	x	●	●	●	●	●
<i>S. planus</i> (Sp)	97		●	●	●	●	●	●	x	x	●	●	x	x	x	●	●	●	●	●	●	●
<i>S. yokoyamai</i> (Syk)	54	65		●	●	●	x	●	●	x	●	●	●	●	●	x	●	●	x	●	●	●
<i>S. yonekurai</i> (Syn)	58	52	68		●	x	●	●	●	●	●	x	●	●	●	●	x	●	●	●	●	●
<i>Eubostrioceras</i> sp. (E)	57	52	52	66		x	●	●	●	●	●	●	●	●	●	●	x	●	●	●	●	●
<i>Scalarites</i> sp. (Scl)	66	74	56	17	29		x	●	x	x	●	●	●	●	x	●	x	x	x	x	●	●
<i>Hyphantoceras</i> sp. (H)	53	45	16	53	31	15		●	●	●	x	x	●	●	●	x	●	●	●	●	●	●
<i>O. perrini</i> (Opr)	02	02	48	99	32	02	0		●	●	●	●	●	●	●	●	●	●	●	●	●	●
<i>Madagascar</i> , cf. <i>ryu</i> (Md)	14	18	08	0	0	17	0	0		●	x	●	●	●	●	●	●	●	●	●	●	●
<i>Scipio</i> , <i>intermedium</i> (Scl)	21	29	14	0	101	22	0	0	0		●	●	●	●	●	x	●	●	●	●	●	●
<i>N. subramosum</i> (Ns)	72	82	53	45	36	76	24	0	11	58		●	●	●	●	●	●	●	x	x	●	●
<i>G. denseplicatum</i> (Gd)	45	54	63	20	67	82	10	07	0	130	77		●	●	x	●	●	●	●	x	●	x
<i>T. glabrus</i> (Tg)	22	29	43	07	51	51	0	06	08	163	63	107		x	x	●	●	●	x	●	●	x
<i>T. epigonus</i> (Te)	12	11	0	0	77	07	0	0	0	0	0	54	29		●	●	●	●	●	●	●	●
<i>A. limatum</i> (Al)	14	13	09	0	39	26	0	0	0	0	0	24	15	0		x	●	●	●	●	●	●
<i>D. ainuanus</i> (Da)	58	56	28	37	44	69	28	06	33	20	57	63	37	06	13		x	●	●	●	●	●
<i>Mesopuzosia</i> sp. (Msp)	24	33	42	31	25	23	0	01	0	217	82	53	64	0	0	09		●	●	●	●	x
<i>M. pacifica</i> (Mp)	09	09	01	0	49	25	0	0	0	0	07	32	37	86	104	19	0		●	●	●	●
<i>M. yubarensis</i> (My)	53	45	16	53	31	15	100	0	0	0	24	10	0	0	0	28	0	0		●	●	●
<i>Subpr. bravaissianus</i> (Sb)	07	04	05	0	04	17	0	0	0	0	13	10	09	0	0	04	0	0	0		●	●
<i>C. woollgari</i> (Cw)	0	01	0	0	0	06	0	0	0	0	04	05	04	0	0	02	0	0	0	0		x
<i>Y. yubarensis</i> (Yy)	02	03	07	0	08	03	0	0	0	100	03	13	15	0	0	01	17	0	0	0	0	19

○: $C_g \geq 0.9$ ●: $0.7 \leq C_g < 0.9$ ●: $0.5 \leq C_g < 0.7$ ●: $0.3 \leq C_g < 0.5$ x: $0.1 \leq C_g < 0.3$ ⊗: $0.1 > C_g \geq 0$

The degree of overlap in occurrence with other species is extremely small in every species of Group C.

These characteristic patterns in the degree of interspecific overlap are closely similar to those produced by cluster analysis using Mountford's (1962) method (see text-fig. 7). If a provisional standard is set as 0.5 on Morishita's index, five groups are distinguished in the twenty-two species examined. Among them, Groups 3 and 5 are composed of the species belonging to Groups A and B. Moreover, most of the species in Groups 1 and 2 have a relatively high value of Morishita's index. None of the species belonging to Group C are included in the five groups.



TEXT-FIG. 7. Dendrogram for interspecific overlap by means of Mountford's (1962) method among the twenty-two species constituting the thirty-two ammonoid samples studied.

DISCUSSION

Presumed habitats and bathymetric distribution of Turonian ammonites in Hokkaido. Boletzky (1977) recently described the differences in mode of life between the post-hatching and adult growth stages in some living cephalopods. In addition, seasonal migration and segregation of size classes and sexes are known in many living cephalopods (Clarke 1969; Westermann 1969; Packard 1972; Clark and Lu 1974, 1975; Hamada and Mikami 1977), and these phenomena probably apply in the case of ammonoids (Westermann 1969; Kennedy and Cobban 1976). If these occurred episodically during the life history, the distribution patterns of living ammonoid populations and thanatocoenoses would probably be more complicated than the simplified model illustrated in text-fig. 1.

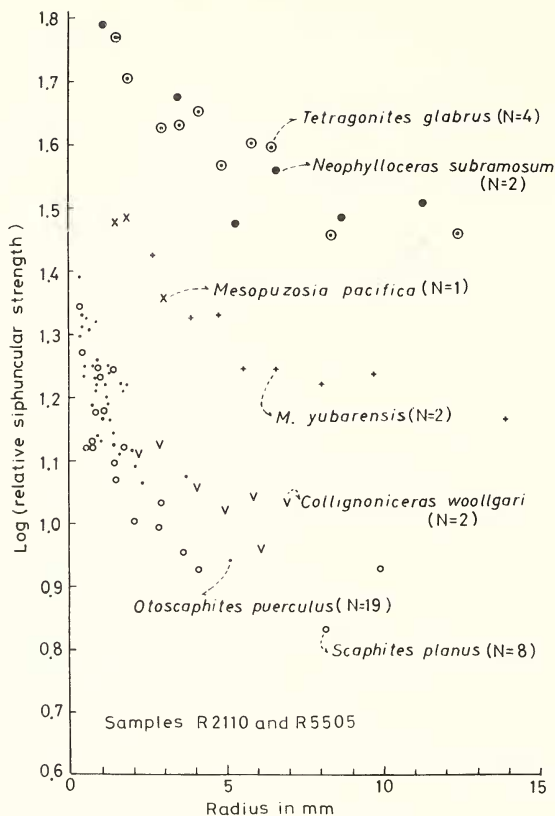
Throughout the investigation of the *Scaphites* facies of the Saku, Obira, and Oyubari areas, significant differences in distribution pattern, mode of occurrence and relationship with lithofacies, and degree of interspecific overlap have been recognized among species constituting the assemblages (text-figs. 3-6; Tables 2, 3). As mentioned above, most of the Turonian ammonites occur abundantly in the inshore to 'intermediate' facies of Matsumoto and Okada (1973) in the western belt of the meridional Cretaceous zone of Hokkaido, while they are rare in the flysch facies in the eastern belt. Collignoniceratids, acanthoceratids, and some scaphitids and baculitids are

restrictedly distributed in the fine-grained sandstone to sandy siltstone lithologies of the Middle to Upper Turonian in the westernmost areas (Pombets, Ikushumbets, Manji, and Yubari areas) (see text-figs. 2, 5; Tanabe *et al.* 1978). Some beds with many ostreids, trigonians, *Glycymeris*, and other shallow-water molluscs, together with numerous drifted plant remains and amber fragments occur in these areas (Matsumoto and Harada 1964; Matsumoto 1965; Obata and Futakami 1977). The majority of the scaphitids, nostoceratids, and diplomoceratids are found abundantly in the western central part of the western belt of the meridional zone of Hokkaido, but they are rare or absent in the eastern belt.

In contrast, species of Tetragonitidae, Phylloceratidae, and Desmoceratidae have a wide geographical distribution pattern from west to east in the marine Cretaceous basin of central Hokkaido, and their habitats could not therefore be determined from the results of assemblage analysis.

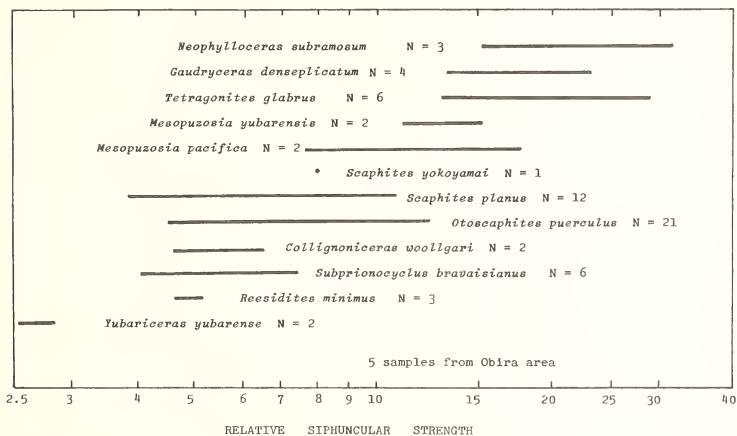
As Westermann (1971) has pointed out, data on relative siphuncular strength may give reliable information in assessing the bathymetry of ammonoids. Denton and Gilpin-Brown (1966, 1973), Collins and Minton (1967), and Raup and Takahashi (1967) have demonstrated that the siphuncular wall of living chambered cephalopods (*Nautilus*, *Spirula*, and *Sepia*) is the mechanically weakest part of the shell. It goes without saying that the siphuncular tube of these animals is sufficiently strong to withstand the hydrostatic pressure at the depths to which they descend; however, there is distinct relationship between the depth limit and the hydrostatic pressure limit of siphuncular implosion in these animals (Denton and Gilpin-Brown 1973, fig. 26). According to Denton and Gilpin-Brown (1966), the hydrostatic strength of the siphuncle in *Nautilus* is related to such factors as the thickness of the siphuncular wall, diameter of the siphuncular tube, and tensile strength of the siphuncular wall material.

In order to determine the bathymetry of ammonoids and to assess the assumed habitats of Turonian ammonoids in Hokkaido based on the results of assemblage analysis, I have examined ontogenetic changes in relative siphuncular strength as measured by Westermann (1971; $100 \cdot Tw/Rs$; Tw : thickness of siphuncular wall, Rs : radius of siphuncular tube) in relation to radius of a spiral for many well-preserved specimens of such species as *Neophylloceras subramosum*, *Gaudryceras denseplicatum*, *Tetragonites glabrus*, *Mesopuzosia pacifica*, *M. yubarensis*, *Scaphites planus*, *S. yokoyamai*, *Otoscapites puerculus*, *Collignonicerus woollgari*, *Subprionocyclus bravaisianus*, *Reesidites minimus*, and *Yubaricerus yubarensis* in five samples selected (R2110, R2113, R6725p, R2003, and R5505; for the location of R5505 see fig. 9 of Tanabe *et al.* 1977) from the Turonian of the Obira area. The radial length of a spiral and siphuncular tube, together with the thickness of the siphuncular wall, were measured along the polished median dorso-ventral or cross-section of each specimen with the aid of a profile projector to an accuracy of 1 micron (magnification at $\times 100$ and $\times 200$). The results are summarized in text-figs. 8, 9. Text-fig. 8 shows that most of the species examined have a greater value for relative siphuncular strength in early to middle growth stages than in later stages. Since the range of variation in strength in each species does not differ greatly among the five samples, all the specimens were probably preserved under virtually the same post-depositional conditions.



TEXT-FIG. 8. Semi-logarithmic scatter diagram showing the ontogenetic change of Westermann's (1971) parameter for relative siphuncular strength in relation to radius of a spiral in the seven selected species among the two ammonoid samples from the Middle Turonian of the Obira area. N = number of specimens of each species.

However, there is a considerable difference in strength among the twelve species examined at the same shell size, and the collignoniceratids and acanthoceratid have less than half the strength of the tetragonitids, desmoceratids, and phylloceratid. If one assumes that the tensile strength of the siphuncular wall material was the same in the twelve species examined, the differences in strength may imply differences in relative depth limits. Judging from the results obtained and the relationship between depth limit and pressure limit of siphuncular implosion in living chambered cephalopods, the depth limits of the tetragonitids, desmoceratids, and phylloceratids may have been much greater than those of the collignoniceratids and acanthoceratids. The scaphitids may have had limits at an intermediate depth.

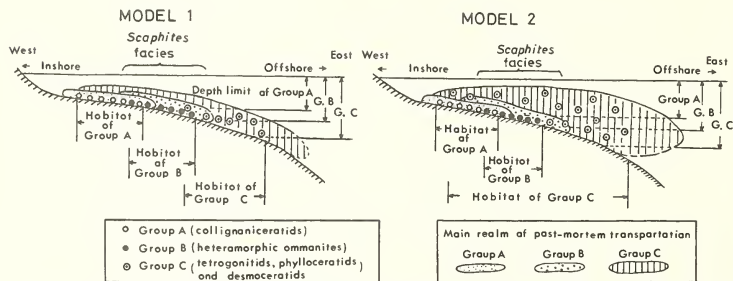


TEXT-FIG. 9. Interspecific variation of relative siphuncular strength among the twelve selected Turonian ammonoid species. The data were obtained from analysis of many well-preserved specimens with radius of a spiral of less than 15 mm collected from five localities of the Obira area. N = number of specimens of each species.

The data obtained on relative siphuncular strength approximate to those of Westermann (1971) obtained from some Mesozoic ammonite genera, and both studies may support the general opinion that the phylloceratids and coiled lytoceratids lived in relatively deeper waters than the ammonitids.

From a consideration of shell buoyancy and swimming ability Mutvei (1975) considered that most ammonoids, apart from a few groups which were adapted to shallow epicontinental seas, lived a planktonic life in the upper 1000 metres of deep oceans. However, the results of assemblage analysis indicate that Mutvei's opinion is unwarranted for some groups of the Turonian ammonites studied.

Effect of post-mortem transportation in the formation of ammonoid thanatocoenoses. As demonstrated above, the collignoniceratids, acanthoceratids, and some heteromorphs in the Hokkaido assemblages have a distinct mode of occurrence and restricted geographical distribution, related intimately to litho- and biofacies. In contrast, such species as *Tetragonites glabrus*, *Gaudryceras densiplicatum*, *Neophylloceras subramosum*, and *Damesites ainuanus*, all of which are smooth or weakly ornate morphotypes, have a wide geographical distribution pattern in the areas studied, with a low frequency of occurrence at many localities regardless of lithofacies types. Also as noted above, the considerable differences in relative siphuncular strength (text-fig. 8) may suggest that all of the tetragonitids, phylloceratids, and desmoceratids inhabited deeper waters than the collignoniceratids, acanthoceratids and some heteromorph ammonites, yet these ammonoids are often found at the same localities in the areas studied.



TEXT-FIG. 10. Two different models to explain the relationship between presumed habitats and extent of post-mortem transportation for several ammonoid groups in Hokkaido in Turonian times.

These observations can be interpreted in one of two ways: (1) the smooth or weakly ornate morphotypes were adapted to wider habitats from inshore shallow water to offshore deep water than the other morphotypes; or (2) post-mortem transport or drift carried them to a wider area, in which case their distribution pattern does not reflect their original habitats. These two possible cases are shown diagrammatically in text-fig. 10.

The extent of post-mortem transportation or drift of ammonoid shells may be estimated indirectly from such data as shell breakage (especially preservation rate of the apertural margin), frequency of epifaunal encrustation on shell surfaces, frequency of specimens with the aptychus or anaptychus in the body chamber, size frequency distribution of a species in an assemblage, and geographical distribution patterns of species. Among the Turonian species examined, breakage of the body chamber is generally rare or slight in the scaphitids, baculitids and other heteromorphs, collignoniceratids, and acanthoceratids. In particular, adult scaphitids,

Eubostrychoceras sp., *Hyphantoceras* sp., and *Nipponites mirabilis* are commonly found in a good state of preservation with the aperture complete (see Tanabe 1977a, b; Matsumoto 1977a). An uncoiled early growth stage with the protoconch is also well-preserved in some specimens of the diplomoceratids and nostoceratids. In contrast, the body chamber is frequently damaged in *T. glabrus*, *G. denseplicatum*, *Neophylloceras subramosum*, and *D. ainuanus*. Epifaunal encrustation was not observed in any of the specimens examined.

Following the work of Lehmann (1970, 1971, 1972, 1975, 1976) and others (e.g. Closs 1967; Kaiser and Lehmann 1971; Schmidt-Effing 1972), aptychi and anaptychi are now regarded as the whole or a part of ammonoid jaws. Therefore, specimens with a pair of aptychi or anaptychi preserved are regarded as undoubtedly autochthonous in a broad sense. *Scaphites planus* and *O. puerculus* are both occasionally found in close association with small aptychi which may have been separated from the body chamber of the two species. Moreover, more than twenty adult specimens of the two species with a pair of aptychus-type jaws in the body chamber have been identified from the Obira and Oyubari areas (Kanie *et al.* 1978). This indicates that the two species never floated for a long distance, or were rapidly waterlogged after death.

Some authors (e.g. Trueman 1941; Mutvei and Reymont 1973; Reymont 1973; Ward 1976; Ward and Westermann 1977) have emphasized that the mode of life of most heteromorph ammonites was planktonic, based on approximate determinations of shell buoyancy. Conversely, such workers as Kauffman (1967), Wiedmann (1969), Hollins (1971), and Kennedy and Cobban (1976) have suggested from the evidence of mode of occurrence and geographical distribution that some adult heteromorphs were benthonic. The mode of occurrence and the restricted geographical distribution pattern of the scaphitids and several other heteromorph species in the marine Cretaceous of Hokkaido may suggest that they never had a planktonic mode of life, or at least in the adult stage. It is possible, however, that the extent of post-mortem transport of such species as *N. subramosum*, *T. glabrus*, *G. denseplicatum*, and *D. ainuanus* might have been much greater than the other Turonian species studied. Consequently, most of the ammonoid assemblages in the Turonian *Scaphites* facies of the Saku, Obira, and Oyubari areas may be regarded as mixed.

Some questions, including possible change of habitat with changing growth stage remain to be resolved in order to complete reconstructions of ammonoid habitats and bathymetric distribution. The present study cannot demonstrate fully whether or not the distribution pattern of smooth or weakly ornate ammonites was strongly influenced by the effect of post-mortem transportation. Further examination of the mode of occurrence and distribution of every species over a wide area is required to resolve this problem, together with functional and comparative morphological analyses of well-preserved specimens of many species.

Acknowledgements. Professors T. Matsumoto, T. Shuto, U. Lehmann, and Dr. W. J. Kennedy are sincerely thanked for critically reading a first draft and for their useful discussions. I also appreciate discussions with Professors G. E. G. Westermann, I. Hayami, and Dr. I. Obata. Miss M. Hayashida assisted in preparing the typescript. This work was supported by the Science Research Fund of the Japanese Ministry of Education, Science, and Culture (No. 274254 for 1977, No. 374257 for 1978) and the Matsunaga Science Foundation, Tokyo.

REFERENCES

- BOLETZKY, S. V. 1977. Post-hatching behaviour and mode of life in cephalopods. Pp. 557-567. In NIXON, M. and MESSENGER, J. B. (eds.). *The biology of cephalopods*. xviii + 616 pp., Academic Press, London. (Symposia of the Zoological Society of London, 38.)
- CHAMBERLAIN, J. A. JR. 1971. Shell morphology and the dynamics of streamlining in ectocochliate cephalopods. *Abstr. Progm. geol. Soc. Am.* 523, 524.
- 1976. Flow patterns and drag coefficients of cephalopod shells. *Palaeontology*, 19, 539-563, pl. 84.
- and WESTERMANN, G. E. G. 1976. Hydrodynamic properties of cephalopod shell ornament. *Paleobiology*, 2, 316-331.
- CLARKE, M. R. 1969. Cephalopoda collected on the SOND Cruise. *Jour. mar. biol. Ass. U.K.* 49, 945-960.
- and LU, C. C. 1974. Vertical distribution of cephalopods at 30° N 23° W in the North Atlantic. *Ibid.* 54, 969-984.
- 1975. Vertical distribution of cephalopods at 18° N 25° W in the North Atlantic. *Ibid.* 55, 165-182.
- CLOSS, D. 1967. Goniatiten mit Radula und Kieferapparat in der Itararé-Formation von Uruguay. *Paläont. Z.* 41, 19-37.
- COLLINS, D. H. and MINTON, P. 1967. Siphuncular tube of *Nautilus*. *Nature, Lond.* 216, 916, 917.
- DENTON, E. J. and GILPIN-BROWN, J. B. 1966. On the buoyancy of the pearly *Nautilus*. *Jour. mar. biol. Ass. U.K.* 46, 723-759.
- 1973. Floatation mechanisms in modern and fossil cephalopods. In RUSSELL, F. S. and YONGE, M. (eds.). *Advances in marine biology*, 11, 197-258. Academic Press, London.
- FISCHER, R. 1967. Zur Ökologie zweier Ammoniten-faunen aus dem Aalenium des Schreibersteins (Berchtesgader Alpen). *Geologica Palaeont.* 1, 175-177.
- HALLAM, A. 1969. Faunal realms and facies in the Jurassic. *Palaeontology*, 12, 1-18.
- 1971. Provinciality in Jurassic faunas in relation to facies and palaeogeography. Pp. 129-152. In MIDDLEMISS, F. A., RAWSON, P. F. and NEWALL, G. (eds.). *Faunal provinces in space and time. Proceedings of the 17th Inter-University Geological Congress*. . . [x] + 236 pp., Seel House Press, Liverpool. (*Geol. J. Spec. Issue*, 4.)
- HAMADA, T. 1964. Notes on the drifted *Nautilus* in Thailand. *Sci. Paps. Coll. Gen. Educ., Univ. Tokyo*, 14, 255-278, pls. 1-5.
- 1965. Post-mortem drift of *Nautilus*. *Venus*, 24, 181-198, pl. 20. [In Japanese.]
- and MIKAMI, S. 1977. A fundamental assumption on the habitat condition of *Nautilus* and its application to the rearing of *N. macromphalus*. *Sci. Paps. Coll. Gen. Educ., Univ. Tokyo*, 27, 31-39.
- HEPTONSTALL, W. B. 1970. Buoyancy control in ammonoids. *Lethaia*, 3, 317-328.
- HOLLINS, J. D. 1971. Occurrence of the ammonite *Ptychoceras adpressum* (J. Sowerby) in the Upper Albian of Kent, England. *Palaeontology*, 14, 592-594.
- JORDAN, R. 1968. Zur Anatomie mesozoischer Ammoniten nach den Strukturelementen der Gehäuse-Innenwand. *Beih. geol. Jb.* 77, 1-64, pls. 1-10.
- KAISER, P. and LEHMANN, U. 1971. Vergleichende Studien zur Evolution des Kieferapparates rezenter und fossiler Cephalopoden. *Paläont. Z.* 45, 18-32.
- KANIE, Y., TANABE, K., FUKUDA, Y., HIRANO, H. and OBATA, I. 1978. Preliminary study of jaw apparatus in some late Cretaceous ammonites from Japan and Sakhalin. *J. geol. Soc. Japan*, 84, 629-631. [In Japanese.]
- KAUFFMAN, E. G. 1967. Coloradian macroinvertebrate assemblages, central Western Interior United States. Pp. 67-143. In KAUFFMAN, E. G. and KENT, H. C. (eds.). *Paleoenvironments of the Cretaceous seaway—a symposium*. Colorado School of Mines, Golden, Colorado.
- KENNEDY, W. J. and COBBAN, W. A. 1976. Aspects of ammonite biology, biogeography, and biostratigraphy. *Spec. Pap. Palaeont.* 17, i-v, 1-133, pls. 1-11.
- KIMOTO, S. 1967. Some quantitative analysis on the chrysomelid fauna of the Ryukyu Archipelago. *Esakia (Hikosan Biol. Lab., Kyushu Univ. Publ.)*, 6, 27-54.
- 1976. Analysis of animal community. Pt. 1. Diversity and species composition. In KITAZAWA, Y. et al. (eds.). *Approaches to ecology*, 14, 192 pp., Kyoritsu Syuppan Book Co., Tokyo. [In Japanese.]
- LEHMANN, U. 1970. Lias-Anaptychen als Kieferelemente (Ammonoidea). *Paläont. Z.* 44, 25-31, pl. 2.
- 1971. Jaws, radula, and crop of *Arnioceras* (Ammonoidea). *Palaeontology*, 14, 338-341, pl. 61.
- 1972. Aptychen als Kieferelemente der Ammoniten. *Paläont. Z.* 46, 34-48, pls. 9, 10.